

# TAXONOMY OF *POGONA* (REPTILIA: LACERTILIA: AGAMIDAE)

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*Pogona* is distinctive and contains six species of moderate to large agamid lizards. *P. barbata*, *P. microlepidota*, *P. nullarbor* and *P. vitticeps* are retained as proposed by Badham (1976). *P. minor* is a widely distributed polymorphic species with subspecies retained in the form proposed by Storr (1982). *P. brevis*, a species similar in size to *P. minor* and *P. nullarbor* but with shorter appendages, is described from the 'black soil' plains of central Queensland. *P. brevis* retains more primitive features than any other species. *P. microlepidota* is closely related to, but distinct from, *P. minor*, *P. nullarbor* and *P. barbata* are the most derived species of the genus, the former probably being closer to their common ancestor in form. Morphological variation within *P. minor* indicates a close relationship with the *Amphibolurus* radiation and *Chlamydosaurus*. An animal similar to *P. minor* is a probable progenitor of both, although the two derived taxa seem to have evolved separately. □  
*Reptilia, Agamidae, Pogona, taxonomy, new species, phylogeny.*

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*Pogona* was described by Storr (1982) to accommodate the bearded dragons, a discrete group of agamids which occur almost Australia-wide, with a single species of the genus in most areas. Once thought of as a widespread polymorphic species, Badham (1976) was able to demonstrate specific differences within the complex, resurrecting *P. vitticeps* from the synonymy of *P. barbata*, and describing several new species. Storr (1982) redefined some of the taxa used by Badham, reducing *P. mitchelli* and *P. minima* to subspecies of *P. minor*. Witten (1982b) suggested *Pogona* evolved from a species similar to *Ctenophorus nuchalis*, but no other phylogenetic relationship has been suggested. An attempt is made here to further stabilise our understanding of the taxa within *Pogona*, and to explore the probable relationships between it and other agamid genera.

## MATERIALS AND METHODS

Meristic characters were recorded with the aid of a binocular dissecting microscope. Labial scales were counted forward from the angle of the mouth, excluding some large scales which continue the 'supralabial' series posteriorly. Subdigital lamellae under the fourth toe were counted from the junction of the third and fourth toe. Where possible, counts are from the right side of the body. For features which vary within a taxon the proportion of specimens scored with the feature is presented as a part of unity (e.g. 0.60 to indicate 60% of specimens with a particular fea-

ture). All features were not scored from all specimens. Specimens used in this study are housed in the Australian Museum, Sydney (AM); Museum of Victoria (NMV); South Australian Museum (SAM); and the Western Australian Museum (WAM).

## SYSTEMATICS

### *Pogona* Storr, 1982

#### DIAGNOSIS

*Pogona* can be distinguished from all other Australian agamids by the presence of spinose scales along the lateral margin of the trunk, and the absence of both vertebral and paravertebral rows of enlarged scales on the trunk.

#### DESCRIPTION

Moderate to large agamids (120-250mm maximum snout-vent length). Short limbs and tail relative to most other agamids. Head deep with blunt snout. Lacrimal bone absent, but lateral process of palatine may intrude into antero-inferior angle of orbit. Preanal and femoral glands widely spaced and arching forward on antero-ventral surface of thigh. Pores usually appear to penetrate skin between scales, but are in fact normally contained within the posterior part of a slightly enlarged scale, commonly appearing in a notch on the posterior margin. Premaxilla narrow, with 3 teeth in adults unless there are replacement teeth developing. Up to 3 pleurodont teeth at the front of both the maxilla and dentary.

Paramarginal scales of lower eyelids with spines which increase in relative size ontogenetically. Gular pouch enlarged. Transverse series of spinose scales at least in lateral gular region, continuing up behind the angle of mouth and tympanum. An occipital crest formed by a series of spines running medially, and at least slightly anteriorly, from about the posterior border of the parietal bone. Temporal series of enlarged scales above tympanum. Scapular tubercle formed by a group of spinose scales at the lateral extension of the gular fold, in front of the insertion of the forelimb. A skin fold from behind the tympanum extends medially to a group of spinose scales on an area of raised skin, either as a fold or tubercle. Nuchal crest is never well developed, but a row of enlarged scales in the nuchal midline is present in some individuals of all species. There may also be a longitudinal paravertebral series of enlarged scales on the neck. Dorsal trunk scales strongly heterogeneous, the central scales much enlarged to form a raised 'farrier's rasp'. Dorsolateral scales much smaller, with scattered spinose scales, and separated from the ventrals by one or more series of spinose scales along the lateral margin of the trunk. Vertebral scale ridge absent. Labials usually smooth, about as long as deep. Loreal scale row obscure in adults. Tympanum large, without scales, at the end of a short meatus restricted postero-superiorly by a skin fold. Canthus rostralis acute to sharply rounded, nares below. Permanent black ventral markings absent; ventral surface marked with dark ocellations. Dorsal colouration consisting of light and dark grey pattern. Colour pattern fades with increase in size. Strongly metachromatic, varying from almost black to light ashen grey in the same individual. Karyotype  $2n = 32$  (12M, 20m).

### *Pogona barbata* (Cuvier, 1829)

*Agama barbata* Cuvier, 1829: 35.

*Pogona barbata* Storr, 1982: 201.

### MATERIAL EXAMINED

AMR17904, AMR21578, AMR25789, no data; New South Wales: AMR59988, AMR59990, East of West Wyalong; AMR59989, 51 km East of Grenfell; AMR59992, 33km SW Hillston; AMR107399-400, AMR107412-3, Upper Horton area; AMR107401, 26 km N Euabalong West; AMR107407-8, AMR107411, 41-50km W Grenfell; NMVD151, Finley; NMVD896, Deniliquin; NMVD14034, 71km W of Moree; NMVD14036, 32km from Moree; Queensland: AMR107397, AMR107402, Emerald; AMR107403, 40m NE Clermont; AMR107404, 25m E Charters

TABLE 1. Meristic characters of *Pogona barbata*.

Scale Count (n)	Mean (SD)	Range
Prenasals (27)	4.63 (0.63)	4-6
Subnasals (27)	4.07 (0.68)	3-5
Internasals (27)	10.30 (1.03)	9-13
Rostral-parietal (26)	14.50 (1.59)	12-18
Suborbitals (27)	4.33 (0.48)	4-5
Supralabials (27)	17.07 (1.24)	14-19
Infralabials (27)	16.26 (1.20)	14-18
Mid-body scales (21)	141.1 (15.6)	101-175
Lamellae (27)	22.74 (1.93)	18-26
Pores (26)	14.62 (2.06)	11-19

Towers; AMR107405, Muttaborra; NMVD137, Fletcher; NMVD8038, Mt Emlyn via Milmerlyn; QMJ49966, 5 km W Alpha; South Australia: AMR20987, Elliston. Victoria: NMVD723, "Goulbourne"; NMVD744, Great Western; NMVD966, Dunolly; NMVD1345; NMVD7934, Big Hill, Bendigo; NMVD14679, Puralka; NMVD14699, Kentbrook State Forest; NMVD48900, 30km South of Kaniva; NMVD57127, 10km ENE of Boort.

### DIAGNOSIS

Distinguished by the presence of a complete multiple gular scale row of spinose scales, an area of spinose scales on the lateral trunk rather than a single interrupted series, and the absence of transverse light lines on the trunk.

### DESCRIPTION

Occipital crests do not meet in the midline, but approach each other obliquely at an angle of about  $120^\circ$  to  $130^\circ$ . Occipital and temporal spine series continue off the posterior dorsum of the head, rather like the cushions of a billiard table, forming two parallel series descending behind the tympanum. Nuchal scale ridge present in about 50% of specimens. Gular scale row complete, formed by several rows of scales about 3 times as long as their base width in adults, the scales a little less attenuated in juveniles. Laterally the gular scale row becomes single and continues up behind the angle of the mouth to meet the temporal series and enclose a triangle of relatively smooth scales behind the tympanum. Spines of these series behind the tympanum are about 3 times as long as their base width. Lower tympanum is often hidden by loose skin. The postauricular skin fold carries spines from the posterior continuation of the occipital series, so the occipital crest forms a loop ending in the paravertebral group of spinose scales. A spine or two between the



FIG. 1. Juvenile *Pogona brevis*. Specimen photographed in Melbourne Zoo.

posterior continuations of the temporal and occipital series may complete, with the gular series, a collar of spines interrupted only in the mid-dorsal region. Another series of spines in the gular region runs posteriorly along the inferior margin of the jaw behind the transverse gular scale row, but in front of the 'normal' gular fold. Scapular tubercle very prominent in large adults. Lateral scale row of trunk composed of scattered spines about 3 or 4 deep. Ventral scales keeled, more prominently in juveniles. Second ceratobranchials absent. Up to 250mm snout-vent length. Table 1 presents meristic data of the species.

#### *Pogona brevis* sp.nov.

##### MATERIAL EXAMINED

**HOLOTYPE:** QMJ32292, adult, Croydon, Queensland. Collected D. Milton in June 1977. Snout-vent length 132mm, tail 141, snout-parietal distance 22.55, Snout-tympanum about 30.8; 15 supralabials, 14 infralabials, 5 scales between nasal and rostral, 5 scales between nasal and supralabials, 11 internasal scales and 18 from rostral to interparietal, 16 lamellae under right fourth toe, 17 under left. Seven preanal and femoral pores (3 left, 4 right).

**PARATYPES:** QMJ38735, Hughenden showgrounds; QMJ38760-1, Hughenden-Muttaborra road, QM J46949, Longreach; NMVD11164, South of Aramac; WAMR9856, Longreach.

**OTHER MATERIAL:** AM field series 11238, 11240, Aramac area; NMVD11165, Richmond; QMJ38762, Hughenden area. A series of animals held in Melbourne Zoo were also examined. The original locality of these animals is not known. Specimens 11238 and 11240 were lent to Richard Wells to assist him in describing the species. Their whereabouts are now not known.

##### DIAGNOSIS

Distinguishable from other *Pogona* by relatively short tail and limbs, and the low number of lamellae under the fourth toe (less than 18). The number of preanal and femoral glands is also reduced relative to other *Pogona* (12 or fewer).

TABLE 2. Meristic characters of *Pogona brevis*.

Scale Count (n)	Mean (SD)	Range
Prenasals (18)	4.39 (0.61)	3-5
Subnasals (18)	3.83 (0.51)	3-5
Internasals (17)	10.88 (0.60)	9-12
Rostral-parietal (17)	16.53 (1.97)	14-21
Suborbitals (17)	4.12 (0.33)	4-5
Supralabials (17)	14.59 (1.18)	13-16
Infralabials (17)	13.71 (1.05)	12-16
Mid-body scales (16)	106.0 (6.08)	97-119
Lamellae (19)	16.47 (1.12)	14-18
Pores (17)	8.18 (1.59)	6-12

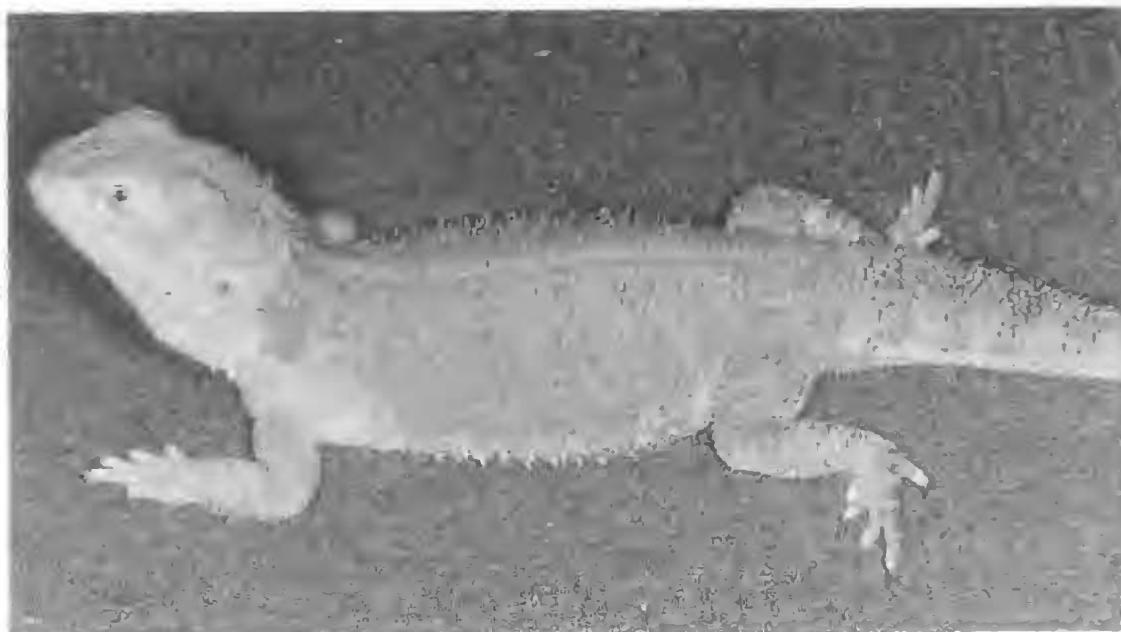


FIG. 2. Adult *Pogona brevis*. Specimen photographed in Melbourne Zoo.

#### DESCRIPTION

Medium-sized, males and females of similar size, adult males averaging 128.0mm SVL (range 91-148) females 130.8 (122-138). The occipital crest is not well developed but transverse, and would meet its fellow at about 150° if the two crests met in the midline. The temporal series approaches the lateral end of the occipital crest but does not continue behind the tympanum. A separate series of spines begins behind the tympanum and runs back to meet the lateral continuation of the gular series to enclose a triangle behind the lower half of the exposed part of the tympanum. The apex of this triangle continues medially as spines on the postauricular fold to a small group of tubercles on the side of the neck. The gular series is very poorly developed and absent in some individuals. The postauricular spines are less than 3 times their base width. Nuchal crest present in only two of 19 specimens examined. Paravertebral nuchal scale row usually present. The scapular tubercle is not well developed. The lateral spines of the trunk are 2 to 3 times their base width. The series is not well developed; there are usually 3 or 4 smaller scales between successive spines. Farrier's rasp condition not well developed, dorsal tubercles more regularly arranged than in other *Pogona*. A small orange area below the tympanum, hidden at times by skin fold. Colour pattern typical of *Pogona*

(Fig. 1), less distinct in larger specimens (Fig. 2). Second ceratobranchials present. Meristic data of the species are presented in Table 2.

#### ETYMOLOGY

From the Latin *brevis* = short, referring to the relatively short limbs, tail, and snout.

#### REMARKS

*Pogona henrylawsoni* Wells & Wellington (1985) cannot be identified from available information. Wells & Wellington's 'diagnosis' apparently includes a description of the holotype, a diagnosis for the species as well as a general description. It is not clear where each of these begins or ends. The description given is not adequate to distinguish *P. henrylawsoni* from other species of *Pogona*. The first diagnostic character given is 'Snout to vent length 130.0mm; vent to tail length 117.0mm'. Taken literally this should exclude all specimens smaller or larger, but even the proportions given would exclude all *P. brevis*; no specimen I examined had an intact tail shorter than the snout vent length. Wells & Wellington (1985) give a full description of the colour pattern, which could apply to any member of the genus. Another 'diagnostic feature' is that *P. henrylawsoni* has smooth ventrals compared to keeled ventrals in *P. vitticeps*. Ventrals in *P. vitticeps* are usually keeled (0.69), but are quite

smooth in some specimens. About half the specimens of *P. brevis* I examined had keeled ventrals. Further, the specimen nominated as the holotype, Australian Museum Field No. 16814, could not be located in a series of specimens donated to the Australian Museum by Wells (Sadleir, pers. comm.). Another specimen mentioned as a '*P. henrylawsoni*', QMJ1051, has apparently been lost (Couper, pers. comm.). There are therefore no known specimens assigned to *P. henrylawsoni* which might act as a guide to the intentions of the authors. As the most common *Pogona* from the type locality of *P. henrylawsoni* is *P. vitticeps*, I treat it as a junior synonym of *P. vitticeps*. A neotype for *P. henrylawsoni* is nominated under the description of that species.

This species is referred to as dwarf bearded dragon. The name is not entirely appropriate, as it attains larger size than *P. minor minor* and *P. nularbor*. However, it is sympatric with both 'giant' species of *Pogona*, and is certainly small relative to those species. A more appropriate name would be 'downs bearded dragon'. People from central Queensland refer to the black soil habitat of *P. brevis* as downs country.

Little is known of the species' ecology. The two specimens I collected were on a dirt road in black soil country. Despite spending several months in the Aramac area I never saw *Pogona* of this size perching on fence posts. It is possible that *P. brevis* defends territory without the normal perching behaviour of other *Pogona*. Almost half the other specimens in museum collections were road kills, also suggesting the species is not obvious to passing herpetologists.

### *Pogona microlepidota* (Glauert, 1952)

*Amphibolurus barbatus microlepidotus* Glauert, 1952: 168.  
*Amphibolurus microlepidotus* Badham, 1976: 439, fig. 4f.  
*Pogona microlepidota* Storr, 1982: 211.

#### MATERIAL EXAMINED

WAMR43028, WAMR56232, Crystal Head; WAMR44258, Mitchell Plateau; WAMR46847, WAMR46962, Prince Regent River National Park; WAMR57108, Bigge Island.

#### DIAGNOSIS

Distinguished by the presence of a multiple lateral scale row, and a weakly developed gular scale row, with no differentially spinose scales in the central throat region.

TABLE 3. Meristic characters of *Pogona microlepidota*.

Scale Count (n)	Mean (SD)	Range
Prenasals (6)	5.50 (0.84)	4-6
Subnasals (6)	4.00 (0.89)	3-5
Internasals (6)	12.00 (0.89)	11-13
Rostral-parietal (6)	19.17 (1.17)	18-21
Suborbitals (6)	4.67 (0.52)	4-5
Supralabials (6)	16.50 (1.38)	15-18
Infralabials (6)	14.17 (1.47)	12-16
Mid-body scales (6)	124.3 (8.57)	116-139
Lamellae (6)	22.67 (0.52)	22-23
Pores (6)	11.50 (1.64)	10-14

#### DESCRIPTION

Gular scale row incomplete, reduced to a few spinous scales below the tympanum. Occipital crest transverse, often on raised skin fold, but not formed by greatly enlarged scales, not extending laterally to meet temporal series nor its fellow in midline. Postauricular fold passes medially to raised area of skin embossed with tubercles; usually a second raised group of tubercles between this and the midline. Ventral and gular scales strongly keeled and mucronate. Lateral scale row of several rows of enlarged spinous scales. Second ceratobranchials present. Up to 180mm snout-vent length (Storr, 1982). Meristic data are presented (Table 3).

### *Pogona minor minor* (Sternfeld, 1919)

*Amphibolurus barbatus minor* Sternfeld, 1919: 78.  
*Amphibolurus minor* Badham, 1976: 436, fig. 4d.  
*Pogona minor* Storr, 1982: 203.  
*Pogona lorae* Wells & Wellington, 1985: 19.

#### MATERIAL EXAMINED

'Typical' *Pogona minor minor*: South Australia; AM R5660-1, Port Lincoln; AMR7658, 407 miles East West line, 30°30'S, 132°09'E; NMVD2657, NMVD2979, NMVD3010, Overland Railway, W of Kychering Soak; NMVD3037, NMVD3052, Overland Railway; NMVD65339, NMVD65379, Wirrula area; NMVD65361, Peterby Tank; SAMR587, Everard Ranges; SAMR5312, Mount Davies; SAMR6556, Yalata Mission; SAMR14482, Maralinga; SAMR14635, Ammaroodinna Hill; SAMR14955A-C, Mt Finke; SAMR14986A-C, Immarna; SAMR15004A-D, Koonibba Mission; SAMR15304, Pinkawillinie Conservation Park; SAMR15506, Emu; SAMR15568, Wyola Lakes; SAMR15569, 74 miles West Vokes Hill; SAMR18132, Muckera Rock Hole; SAMR18133, Serpentine Lakes; SAMR18168-9, Wyola Lakes; SAMR18376, Vokes Hill Junction; SAMR21374, Bates; SAMR22914-5, Yalata Mission area; SAMR24479, Goog's track;



SAMR25427, 45 Canegrass Swamp; SAMR25428, Mt Ive Homestead; SAMR25673, 51km NW Yalata Rockhole; SAMR26389, 99km NW Cook; SAMR26809, Mabel Creek homestead; SAMR28437, 45km NNE Minnipa; SAMR28525, 100km NE Minnipa; SAMR30083, Yalata; SAMR31872, SAMR31875, Mt Finke; SAMR31916, SAMR31923, Pinjarra Dam; SAMR31939-40, Wallala Hill; SAMR31961, Inila Rock Waters, Yumbarra Conservation Park; SAMR31989, Yumbarra Rock Hole; SAMR32011, SAMR32019, Mitcherie Rock hole; SAMR32036-8, SAMR32073, SAMR32076, SAMR32095, Immarina Siding; SAMR32142, SAMR32146, SAMR32165, SAMR32174, Maralinga; SAMR32189, 47km N Muckera Rockhole; SAMR32205, SAMR32214, SAMR32218, SAMR32279, 50km SW Halinor Lake; SAMR32288, 29km N Muckera Rockhole; SAMR32312, Mt Christie Siding; SAMR32613, Two Tj Bore; SAMR32622, Tallaringa Well; SAMR33983, Mt Finke; SAMR36226, Curtin Springs homestead; SAMR37656, 39km S Kokatha homestead, Northern Territory; AMR15182, Haast's Bluff, Macdonnell Range; NMVD493, Illamurta; SAMR322, Macdonnell Ranges; SAMR4820, Mt Liebig; SAMR9520, Yuendumu; SAMR29903, Curtin Springs homestead; WAMR34182, Armstrong Creek; WAMR34197-8, Lasseter's Cave; WAMR45206, Docker River; WAMR46634-5, Ayer's Rock, Western Australia; SAMR1402A-D, between Ashburton and Gascoyne Rivers; WAMR19568, Ullawarra; WAMR31004, Mount Tom Price.

*Pogona minor* 'minima' morphs: Western Australia; AMR133759, Gibson; AMR133915, AMR133988, Salmon Gums; AMR136236, Nedlands; AMR136239, Lesmurdie; NMVD772-4, King George Sound; NMVD2435, Katanning; NMVD8002, Bunbury; SAMR22836, Yanchep; WAMR23812, Field's Find; WAMR37737, 29km ENE Paynes Find; WAMR87461, Lake Mason homestead.

*Pogona minor* 'minima/minor' intermediates not used in preliminary analyses: AMR134278, AMR134565, Gnarlou Bay; AMR134313, AMR134584, Point Quobba; AMR136238, Vlaming Head; AMR136240, 57m NE Fraser Range turn-off, Nullarbor Plain; SAMR25494, 87km NW Cook; SAMR25577, 82km NW Cook; SAMR25678, 50 km W Yalata rockhole; NMVD783-5, Minilya; NMVD976, Stanton Springs; NMVD1778, Middalya; NMVR849, NMVR852, NMVR1005, NMVR1007, NMVR1011, (?)Perth; WAMR16867-71, Ningaloo; WAMR19567, Wittenoom; WAMR24829, Lander; WAMR29965-7, Overlander; WAMR69679, Mount Bruce; WAMR70808, Dirk Hartog Island; WAMR78246-7, Boollogooro.

*Pogona minor* 'minima' morphs not included in analyses: NMVD630, NMVD664-8, NMVD782, NMVD3405, Western Australia; NMVR848, NMVR1002, NMVR1004, NMVR1006, NMVR1008, (?)Perth.

TABLE 4. Meristic characters of *Pogona minor minor*.

Scale Count (n)	Mean (SD)	Range
Prenasals (78)	4.79 (0.81)	3-7
Subnasals (78)	3.82 (0.58)	2-5
Internasals (77)	10.13 (1.22)	7-13
Rostral-parietal (74)	13.92 (1.29)	12-18
Suborbitals (77)	3.84 (0.48)	3-5
Supralabials (81)	15.79 (1.30)	13-19
Infralabials (81)	14.65 (1.28)	11-17
Mid-body scales (35)	109.7 (7.60)	99-127
Lamellae (78)	23.81 (2.26)	16-28
Pores (101)	13.42 (1.75)	10-18

# DIAGNOSIS

*P. minor* is distinguishable from other *Pogona* by the presence of gular scales similar to ventrals, without a transverse series of more spinose scales at the centre of the throat; a single interrupted series of spinose scales along the lateral margin of the trunk, and a relatively long tail (at least 160% of snout-vent length). *P. m. minor* has a weaker occipital crest and narrower head than at least adult *P. m. mitchelli*, and shorter appendages than *P. m. minima*.

# DESCRIPTION

Occipital crest transverse, but not strongly developed. Temporal series of spines does not continue much behind level of tympanum. The postauricular skin fold ends medially in a variable paravertebral structure. From the north and east of the species' range there is a raised area of skin supporting a clump of tubercles, often in the form of a large single scale surrounded by smaller spines. Specimens from the west of the species' range have a skin fold running forward from the medial end of the postauricular fold carrying a more or less longitudinal row of tubercles. Nuchal scale ridge often present (0.60). Gular scale row incomplete. Ventrals weakly keeled (0.60) or smooth, gulars weakly keeled (0.30) or with a rounded surface. Preanal and femoral glands much more active in males than females. Second ceratobranchials present. Up to 145mm snout-vent length (Badham, 1976). Table 4 presents meristic data of the nominate subspecies, including specimens from the south-west of Australia.

# *Pogona minor minima* (Loveridge, 1933)

*Amphibolurus barbatus minimus* Loveridge, 1933: 69.  
*Amphibolurus minimus* Badham, 1976: 437.  
*Pogona minor minima* Storr, 1982: 208.

TABLE 5. Meristic characters of *Pogona minor minima*.

Scale Count (n)	Mean (SD)	Range
Prenasals (16)	4.44 (0.51)	4-5
Subnasals (16)	3.06 (0.25)	3-4
Internasals (16)	9.50 (1.32)	7-13
Rostral-parietal (16)	12.75 (1.18)	11-15
Suborbitals (16)	3.13 (0.34)	3-4
Supralabials (16)	14.00 (1.03)	12-16
Infralabials (16)	13.63 (0.81)	12-15
Mid-body scales (11)	100.3 (9.46)	82-120
Lamellae (16)	24.69 (1.62)	22-28
Pores (12)	14.58 (1.83)	12-17

## MATERIAL EXAMINED

WAMR19501-16, West Wallabi Island.

## DIAGNOSIS

Distinguished from the nominate subspecies by the possession of longer appendages, the forelimb length falling from about 50% to 44% of snout vent length during growth (44% to 37% for *P. m. minor*), and from *P. m. mitchelli* by a much narrower head (less than 23% of snout vent length in large adults) and weak development of the occipital crest.

## DESCRIPTION

Postauricular fold medially joins a longitudinal skin fold with a series of enlarged spines. Labial scales frequently carry a longitudinal ridge, particularly the posterior supralabials. All scales keeled, gulars weakly. Up to 115mm snout-vent length (Storr, 1982). Meristic data are presented in Table 5.

## REMARKS

Badham (1976) treated both *P. m. minima* and *P. m. mitchelli* as full species. Storr (1982) reduced both to subspecies of *P. minor*. Storr also altered the boundary between *P. minima* (of Badham) and *P. minor*, restricting *P. m. minima* to the type locality of the holotype, the Houtman Abrolhos Islands.

Badham (1976) used the presence of a 'distinct nuchal row of 5 or 6 spines parallel to and on either side of the vertebral column' as the main feature characterising *P. minima*. Using this character, I sorted mainland specimens into 'minima' morphs and *P. m. minor*. Animals intermediate in morphology or distribution were excluded. Analyses of morphometric and meristic data were carried out. The morphometric data are discussed

elsewhere (Witten, 1994), and the meristic data are presented in Table 6.

Storr (1982) used the higher number of lamellae under the fourth toe as one feature helping to distinguish *P. m. minima* from *P. m. minor* on the adjacent mainland. My data show a lower number of lamellae in the mainland 'minima' morph group, but the number of lamellae in *P. m. minor* from other areas is close to identical to that of *P. m. minima*. Storr's data had a slightly higher mean for Houtman Abrolhos animals (25.3) and a lower one for mainland *P. m. minor* (22.8) than I recorded, but even Storr's data could only be used diagnostically at the extremes of his recorded ranges. Other data recorded do not show any significant difference between groups. There is a tendency for Houtman Abrolhos specimens to have fewer scales between the labials and both the orbit and nasal scale. The number of labial scales is lower in the island population, but there are more preanal and femoral glands (Table 6). Both these trends are consistent with Storr's data. The meristic data do not show a consistent trend indicating whether the mainland 'minima' animals should be grouped with *P. m. minor* or *P. m. minima*. However, analyses of morphometric data support Storr's position (Witten, 1994). The data presented with the description of *P. m. minor* include all mainland specimens examined, apart from those assigned to *P. m. mitchelli*.

TABLE 6. Meristic characters of *Pogona minor*. Numbers in each column are mean (SD) and range.

Count	<i>P. m. minor</i>	<i>P. m. 'minima'</i> mainland	<i>P. m. minima</i>
Prenasals	4.86(0.78) 3-7	4.43(0.85) 3-6	4.44(0.51) 4-5
Subnasals	3.82(0.57) 3-5	3.71(0.73) 2-5	3.06(0.25) 3-4
Internasals	10.23(1.26) 8-13	9.64(1.22) 7-12	9.50(1.32) 7-13
Rostral-parietal	13.98(1.33) 12-18	13.64(1.43) 12-16	12.75(0.18) 11-15
Suborbitals	3.80(0.48) 3-5	3.93(0.47) 3-5	3.13(0.34) 3-4
Supralabials	15.90(1.32) 13-19	15.14(1.10) 13-17	14.00(1.03) 12-16
Infralabials	14.77(1.20) 12-17	14.14(1.29) 11-15	13.63(0.81) 12-15
Mid-body scales	110.6(7.3) 99-127	102.8(1.8) 101-105	100.3(9.5) 82-120
Lamellae	24.11(2.05) 19-28	22.69(3.15) 16-28	24.69(1.62) 22-28
Pores	13.54(1.72) 10-18	12.85(2.03) 9-16	14.58(1.83) 12-17

TABLE 7. Meristic characters of *Pogona minor mitchelli*.

Scale Count (n)	Mean (SD)	Range
Prenasals (30)	4.67 (0.71)	3-6
Subnasals (30)	4.30 (0.75)	3-6
Internasals (30)	10.97 (1.33)	9-13
Rostral-parietal (30)	15.10 (1.94)	11-20
Suborbitals (30)	4.17 (0.65)	3-6
Supralabials (30)	15.80 (1.30)	14-19
Infralabials (30)	14.87 (1.11)	13-17
Mid-body scales (14)	110.6 (9.20)	90-122
Lamellae (30)	22.10 (1.7)	19-27
Pores (28)	13.21 (1.87)	10-18

***Pogona minor mitchelli* (Badham, 1976)**

*Amphibolurus mitchelli* Badham, 1976: 435, fig. 4c.  
*Pogona minor mitchelli* Storr, 1982: 209.

**MATERIAL EXAMINED**

PARATYPES: Northern Territory: SAMR1399-1400, SAMR1404, Tennant Creek; SAMR3546, Yuendumu. Western Australia: SAMR3436, Pilgangoora Well; WAMR13066, Mount Edgar; WAMR15823, Derby; WAMR19377, Mundabullangana.

OTHER MATERIAL: Northern Territory: SAMR15622, Yuendumu. Western Australia: AMR38712, 11m W Springvale; AMR100912-5, AMR101470-1, AMR101550, Sandfire Flat roadhouse; NMVD999, Broome; NMVD1000-1, Marble Bar; WAMR45758-60, Mount Edgar; WAMR46068, 63km ENE de Grey River crossing; WAMR50696, Drysdale River National Park; WAMR68983, 24km E Deep Creek; WAMR79111-2, Broome; WAMR87344, Mandora homestead.

OTHER SPECIMENS (examined, but not used in analyses): SAMR4483, Tambrey; SAMR4484, Kangiangi, W.A.; WAMR20078-9, Tambrey, W.A. (These specimens are all paratypes of *Amphibolurus mitchelli*, but are actually *P. m. minor* - see Discussion); NMVD33, NMVD2949, Tennant Creek N.T.; NMVD494, Ilamurta, N.T.; NMVD1480, Derby, W.A.; NMVR847, NMVR850, NMVR1009-10, Perth(?), W.A.

**DIAGNOSIS**

Distinguished mainly by the possession of a prominent transverse occipital crest similar to *P. vitticeps*, and a relatively wider head and larger ear aperture than other *P. minor*.

**DESCRIPTION**

Similar in most respects to *P. m. minor*. Ventrals weakly keeled (0.67) or smooth, gulars weakly keeled (0.33) or with a rounded surface.

Up to 171mm snout-vent length. Meristic data of the subspecies are presented in Table 7.

***Pogona nullarbor* (Badham, 1976)**

*Amphibolurus nullarbor* Badham, 1976: 440, fig. 4g.  
*Pogona nullarbor* Storr, 1982: 212.

**MATERIAL EXAMINED**

PARATYPES: WAMR16888, WAMR16896, Forrest; WAMR24655, Cocklebidy; WAMR28127, Wilson Bluff; WAMR31964-5, 112 km NNE Rawlinna.

OTHER MATERIAL: South Australia: SAMR5034, Eyre Peninsula or Nullarbor Plain; SAMR14313A-B, 29km S Watson; SAMR14314, Watson; SAMR15570, 10m E Cook; SAMR18170, SAMR19807, SAMR20106, SAMR22290, SAMR23939-41, SAMR25298-301, 20km E Nullarbor homestead; SAMR23005, 125km E SA/WA border; SAMR26171, 13km NE Border Village; SAMR26393, SAMR26395, 12km NW Hughes; Western Australia: SAMR5437, Madura; SAMR23029, 53km E Madura; WAMR91743, 16km SSE Haig; WAMR91831, 28km NNW Middini Beach; WAMR91832, Haig; WAMR91870, 26km ESE Madura; WAMR91924, 19km S Yuwanyandi rock-hole.

**DIAGNOSIS**

Similar in scalation to *P. barbata*, from which it may be distinguished by the presence of narrow pale transverse stripes on the body, and much more obvious ventral patterning. The tail and limbs are relatively shorter.

**DESCRIPTION**

Spines and tubercles of the head region very similar to *P. barbata*, including a complete gular scale row, and the occipital and temporal series descending behind the tympanum. Second ceratobranchials absent. Ventral pattern more strongly developed than in other *Pogona*, forming

TABLE 8. Meristic characters of *Pogona nullarbor*.

Scale Count (n)	Mean (SD)	Range
Prenasals (33)	4.64 (0.70)	3-6
Subnasals (33)	3.61 (0.66)	3-5
Internasals (33)	11.42 (0.97)	9-13
Rostral-parietal (32)	15.63 (1.16)	13-18
Suborbitals (33)	3.85 (0.51)	3-5
Supralabials (32)	15.53 (1.19)	13-18
Infralabials (33)	14.06 (1.09)	12-16
Mid-body scales (29)	108.7 (8.45)	91-125
Lamellae (33)	20.39 (1.22)	17-23
Pores (33)	12.82 (1.69)	10-16



distinctive longitudinal streaks on the gular surface, and the ventral ocellations often coalescing to form irregular streaks on the ventro-lateral surface of the trunk. Preanal and femoral glands active in both sexes. Up to 144mm snout-vent length. Table 8 presents meristic data of the species.

### *Pogona vitticeps* (Ahl, 1926)

*Amphibolurus vitticeps* Ahl, 1926: 189.

*Pogona vitticeps* Storr, 1982: 201.

*Pogona henrylawsoni* Wells & Wellington, 1985: 19.

#### MATERIAL EXAMINED

New South Wales: AMR15296, Byrock; AMR47319, Wanaaring; AMR59991, AMR59996-7, AMR107409-10, AMR107444, Roto area; NMVD12164, Mooma; NMVD52088-9, Broken Hill, Northern Territory: NMVD8970, Plenty River, near Dinkum Mine. Queensland: AM Field tag 11252, 30m WSW Aramac; AMR17122-3, Cunnamulla; AMR107398, Isisford; AMR107406, Aramac; NMVD14181, Dajarrah; NMVD58570, Hammond Downs, near Windorah. South Australia: AMR13904-5, Simpson Desert; AMR21077, Lake Eyre; NMVD1123, Lake Eyre; NMVD3072, NMVR4547-8, Purnong; NMVD41501, Billeroo Creek; NMVD41502, Coolibah Dam; NMVD13781-2, Mulka, via Marree. Victoria: NMVD648, Gawler Ranges(?); NMVD699-700, Raak Plains; NMVD777, NMVD970, NMVD1031, NMVD1036, NMVR4855, Ouyen; NMVD787, Red Cliffs; NMVD7871, Mt Hope; NMVD11753-4, Landraak Plain, near Hattah; NMVD15379, Lindsay Point Station; NMVD15382, Mildura; NMVD18220, 53km S Murrayville; NMVD47858, Millewa South Bore; NMVD52637, 3km NNW Chinaman Well; NMVD52742, Ross's Spring, 23km S Tutty; NMVD53482, NMVD53827, NMVD53836, NMVD53853, NMVD53907, NMVD53925, NMVD54051, NMVD54070-1, NMVD54123, NMVD54131-2, NMVD54144, NMVD54557, NMVD54749, NMVD54754, NMVD54759-60, NMVD54789, NMVD54790, NMVD55036, NMVD55064, NMVD55251, NMVD55305, NMVD55583, NMVD56741, Chinaman Well area; NMVD58472, NMVD58477, 30km WNW Kiamil; NMVD58501, NMVD58548, NMVD58555, NMVD59448, NMVD59818, Milmed Rock area; NMVD60324-5, NMVD60609, NMVD60694-5, NMVD60708, NMVD60741, NMVD60760, NMVD60762-3, NMVD60768-9, NMVD60778, NMVD60785, NMVD60826-8, NMVD60841, NMVD60854, near Sunset Tank.

#### DIAGNOSIS

Distinguished by the possession of complete transverse gular scale row and a single lateral scale row. Tail short relative to *P. minor*, about

150% of snout vent length in hatchlings falling to 120% in adults.

#### DESCRIPTION

Occipital crests approach each other at an angle of about 140° to 150°. Occipital and temporal spine series meet laterally, a little behind the tympanum. There is usually a small gap below this point to a group of spines extending from behind the tympanum. Gular scale row complete, formed by several rows of scales about twice as long as their base width. Laterally the gular scale row becomes single and continues up behind the angle of the mouth to meet the postauricular series and enclose a triangle of relatively smooth scales behind the tympanum. Spines of these series behind the tympanum are about 3 times as long as their base width. At the posterior apex of the triangular series the postauricular fold runs medially to a group of tubercles. Lateral scale row of trunk composed of stout spines in a single row. Nuchal scale ridge usually present (0.91). Ventrals usually keeled (0.76), gulars keeled (0.69), or with a rounded surface, keels becoming less pronounced ontogenetically. Second ceratobranchials present. Up to 247mm snout-vent length. Meristic data are presented in Table 9.

#### REMARKS

For reasons outlined under *Pogona brevis*, I nominate a neotype for *P. henrylawsoni* at this point: AMR143896, 34.4km N of Barkly Highway via Normanton Road, R. Sadler, G. Shea 6 Apr 1994. It is a little larger than the lost holotype (145mm snout vent length, versus 130), and has an entire tail, but otherwise agrees well with the description of Wells and Wellington (1985). The gular scale row is poorly developed, the ventrals are very weakly keeled, and the colour pattern matches the description entirely, except that the

TABLE 9. Meristic characters of *Pogona vitticeps*.

Scale Count (n)	Mean (SD)	Range
Prenasals (81)	4.93 (0.75)	3-7
Subnasals (81)	4.38 (0.68)	3-6
Internasals (81)	11.09 (1.14)	8-13
Rostral-parietal (80)	14.79 (1.59)	11-20
Suborbitals (81)	4.37 (0.49)	4-5
Supralabials (81)	16.99 (1.12)	15-20
Infralabials (81)	15.96 (1.19)	13-19
Mid-body scales (22)	140.1 (11.1)	119-164
Lamellae (80)	21.78 (1.51)	18-26
Pores (78)	14.53 (1.97)	9-19

five dumbbell light marks are placed a little further anteriorly, with the first over the axilla, rather than the last over the groin. The locality is about 100km west of the original type locality, but this specimen came nearest to meeting the requirements of the code for nomination of neotypes. The new type locality is also in 'black soil' country specified by Wells and Wellington as the habitat of *P. henrylawsoni*.

#### MORPHOLOGICAL VARIATION

Storr (1982) claimed *Pogona* was distinguishable from *Ctenophorus* by 'alignment of pre-anal pores backwards towards the midline'. In fact this feature is common in only *P. minor minima* and *P. m. minor* from the adjacent mainland. Storr's diagnosis, strictly applied, would exclude all species assigned to the genus except some *P. minor*. The preanal pores of some *P. m. mitchelli* (e.g. AMR101470, WAMR45759) are more or less parallel with the vent, and in a separate series from the femoral pores. However, the arrangement of pores in other *Pogona*, including most *P. m. mitchelli*, is more or less identical to that found in *Ctenophorus nuchalis*, the feature used by Storr (1966) to distinguish between it and the otherwise very similar *C. reticulatus*.

The pore arrangement in some *P. m. minima* deserves special comment. Within this small island population the full range of variation in pore arrangement can be found. Individuals vary from the 'nuchalis' pattern (WAMR19506) through to an arrangement very similar to that found in *Amphibolurus* (WAMR19505) (Fig. 3).

The dentition of all *Pogona* is similar. Hatchlings have a single median 'egg' tooth. This is followed by a small tooth on either side of the premaxilla, and then a central tooth erupts. Premaxillary teeth are usually considered pleurodont (Cooper et al., 1970), as are the most anterior teeth on both the maxilla and dentary in adults. The anterior dentary and maxillary teeth are caniniform, resembling the canines of carnivorous mammals. These teeth are also absent in hatchlings, appearing later in development. The attachment to the bone tends to be slightly lateral to the line of the acrodon teeth row. In skeletal material they are embedded within the bone, and successional may be a better descriptor than pleurodont. In adults the anterior successional teeth interlock when the mouth is closed. The most anterior dentary tooth passes into the gap between the median and lateral premaxillary tooth. More posterior teeth continue this meshing, but the arrangement is sometimes irregular.

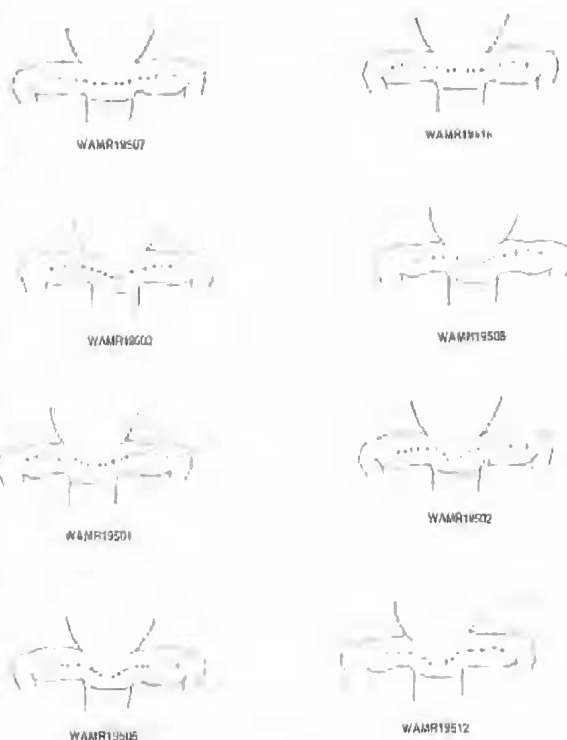


FIG. 3. Variation of pore arrangement in specimens of *P. minor minima*. Note the variation from a '*Ctenophorus nuchalis*' arrangement in WAMR19506 to an '*Amphibolurus*' arrangement in WAMR19505.

Successional teeth are replaced by larger teeth during growth. This is apparent in some specimens, where more than the usual number of teeth are present, and the 'bite' may be temporarily unorthodox.

The tympanum in *Pogona* is below the level of the surrounding skin, at the bottom of a short meatus. The tympanum is ontogenetically further concealed by the development of a skin fold over the postero-superior part of the tympanum. This fold is small in hatchlings, at first flattening the postero-superior margin of the tympanic opening to make it roughly triangular. As the animal grows, more of the tympanum is covered. In some adults more than half the tympanum is covered, and the 'ear' aperture is oval and much smaller than the contained tympanum.

The occipital crest in most species closely approaches or joins the temporal spine series laterally so that the posterior part of the head is surrounded by a triangular series of spines. This is prominent in *P. vitticeps* and *P. m. mitchelli*, and in these taxa there is usually a gap between

the corner of the triangle and the postauricular spines. The arrangement is similar, but less prominent in other *P. minor* and in *P. microlepidota* and *P. brevis*. In the latter two species the occipital series does not usually join the temporal series. In *P. barbata* and *P. nullarbor* the occipital and temporal series continue down behind the tympanum in parallel series. Variations in these spine arrangements were the main features used to distinguish species in Badham's (1976) revision of the genus.

The labial scales in most *Pogona* are smooth, but most *P. m. minima* have labial scales with a longitudinal ridge. This feature is also present in many mainland *P. minor* of both other subspecies, and in all *P. minor* the ridge tends to be better developed in the supralabial series. Some *P. microlepidota* have a faint ridge on the supralabial scales, and some small *P. nullarbor* specimens also had some indication of a ridge on the supralabials. Otherwise the character is confined to the subspecies of *P. minor*.

One feature distinguishing *Pogona* from most other Australian agamids is the presence of a row of spines on the paramarginal scales of the lower eyelid. This row of spines is shared with the burrowing *Ctenophorus* of the *C. reticulatus* species group (Witten, 1982b). The spines of this row become more prominent ontogenetically, the best developed spines appearing in the largest specimens. This correlation with size crosses species boundaries to some extent. Very small *C. clayi* (the smallest species with the feature), for example, having only rudimentary spines (Witten, 1982a). Within *Pogona* there is some variation apart from that expected from size. The spines are less well developed in *P. vitticeps*, particularly from the south of its range. The smaller animals from the Big Desert (Witten & Coventry, 1990) have weaker spines than *P. m. minor* of comparable size. *P. m. minor* from the Western Australian coast and *P. m. minima* also have less well-developed spines, with some adult specimens having little more than triangular ridges on the paramarginal scales.

Most Australian agamids have subdigital lamellae which are smooth centrally with a lateral projection on either side. All *Pogona* species have individuals with this condition. A common variation includes the distal few lamellae having four ventral projections rather than two. This condition is particularly common in *P. m. mitchelli*, with more specimens having four spines than two. Some specimens of all *Pogona*

taxa exhibit variation in the number of spines on the subdigital lamellae.

All living *Pogona* I examined had some indication of yellow pigmentation in the mouth lining. This is variable, and Bradshaw (1970) commented that northern populations of *P. m. minor* had a white lining, while southern populations had the more typical yellow pigmentation. I have not examined living specimens of *P. microlepidota*.

The glands secreting through the preanal and femoral pores are subject to some sexual dimorphism in *Pogona*. *P. minor* may be sexed with reasonable reliability by the differential enlargement of the pores in males. The pores in females are not increased in relative size from hatchlings (0.1–0.2 mm), but in males are obviously more active and enlarged (0.4–0.65 mm). The same is not true of other species of the genus. In *P. nullarbor* pores are of a similar size in both sexes, and are clearly actively secreting at a similar level. In other species pores are more variable in size, usually more active in males, but the sex difference seen in *P. minor* is not as pronounced.

The colour of *Pogona* has often been described as reddish or brown, as well as the more common grey. All species with which I am familiar are patterned in shades of grey, with the single exception that there is often a small orange flash beneath the tympanum. Animals which are in the process of shedding their skin often have a distinct contrast between the old and new skin. Apparently the 'old' skin becomes dusty, picking up local soil to allow better colour matching with their normal background. Most animals which appear to be brown or red are probably from areas with soil of that colour.

## DISCUSSION

*Pogona minor* is a wide-ranging species containing three main morphs. These were considered as separate species by Badham (1976), but were reduced to subspecies by Storr (1982), who also redefined the boundary between *P. minor minor* and *P. m. minima*. Badham referred specimens from the south west corner of the continent to *P. minima*, while Storr restricted *P. m. minima* to the type locality of the holotype (Houtman Abrolhos Islands). There is merit in both boundaries. Storr is clearly correct in reducing *P. minima* to subspecific rank. The population on the Houtman Abrolhos closely resembles morphologically *Pogona* on the adjacent mainland. This mainland population intergrades into typical

*P. m. minor* as the climate becomes increasingly arid moving both north and east from the south west corner. Meristic features do little to resolve whether Badham's or Storr's boundary should be preferred (Table 6). Mainland *P. minima* are generally intermediate between Houtman Abrolhos and central Australian animals. However, in the number of lamellae under the fourth toe the mainland '*minima*' morphs have a lower count than either eastern *P. m. minor* or typical *P. m. minima*. This may have influenced Storr in nominating subdigital lamellae as an important diagnostic feature separating *P. m. minor* from *P. m. minima*, particularly because he examined almost exclusively Western Australian specimens (7 specimens from N.T., 4 from S.A.). Morphometric data show a much clearer separation between mainland '*minima*' morphs and typical *P. m. minima* (Witten, 1994), there being little morphometric difference between mainland '*minima*' and *P. m. minor*. Even morphometric data, however, will only allow the separation of most specimens. The presence of this east-west cline within *P. minor* demonstrates continuing gene flow between the different populations. The recognition of *minima* as a race might be more appropriate. I would prefer to leave the nomenclature as stable as possible, and the present status of this taxon is at least defensible, given geographic isolation of the most westerly animals.

There is a second cline within *P. minor*. Apart from the east-west cline towards *P. m. minima* in the west, there is a north-south cline with *P. m. mitchelli* in the north. The distinction between these subspecies is much better defined. Storr (1982) had more specimens than Badham (1976), and was better able to define the boundary between *P. m. minor* and *P. m. mitchelli*, having first recognised that *mitchelli* represented a subspecies of *P. minor*. Four paratypes of *Amphibolurus mitchelli* should be considered *P. m. minor*. Two of these, WAM20078-9 from Tambrey, Storr reassigned to *P. m. minor* without comment. They are simply listed among specimens examined. The tags on these specimens, incidentally, do not have the normal 'R' prefix on other reptile specimens in the Western Australian Museum. Two South Australian Museum specimens, also from Tambrey or near it (SAMR4484 is from Kangian-gi), were listed as paratypes of *A. mitchelli* (Badham, 1976). One, SAMR4483, I identified as *P. m. minor* not realising at the time that it was a type of *A. mitchelli*. The other specimen, SAMR4484,

examined as a series of *P. m. mitchelli*, has its occipital crest on a raised skin fold. My notes on the specimen included the comment 'nearer *minor* than *mitchelli*'. All four of these specimens have occipital crests of relatively small spines. All are sexually mature with wide heads, but no wider than typical *P. m. minor*.

Three specimens of *P. nullarbor* are quite different (SAMR23939-41). Normal *P. nullarbor* have an arrangement of the occipital and temporal spines similar to *P. barbata*, but these animals closely resemble *P. m. mitchelli* in these features. They also have a single lateral series of spines. They are identifiable as *P. nullarbor* because they have a complete gular scale row, and the strongly developed ventral pattern is also characteristic of *P. nullarbor*. These specimens were all hatchlings from a clutch laid in captivity by SAMR18581, reported by Smith & Schwaner (1981). Other hatchlings from the same clutch (SAMR19807, SAMR20106, SAMR25298-301) were typical *P. nullarbor*. All of these specimens were kept in captivity for varying periods. It is possible that the conditions under which they were kept influenced their morphology.

#### PHYLOGENY

*P. brevis* appears to be the most primitive member of the genus, if only because it is least divergent from the presumed ancestor of the genus, a species resembling *Ctenophorus nuchalis*. The 'farriers rasp' condition of the dorsal scales is least developed in *P. brevis*, and its short appendages and rounded head resemble *C. nuchalis*. Its relationship to other species of the genus is unclear.

*P. minor* might be nearest the main stock of *Pogona*, a widespread variable species with several morphs. It appears some of these morphs have become fixed and evolved into distinct species. *P. vitticeps* is very close to *P. m. mitchelli* in morphology, differing mainly in the possession of a 'beard' and larger adult size. The Pleistocene Lake Dieri may have acted as an isolating mechanism between *P. m. mitchelli* in the west and *P. vitticeps* in the east in the way suggested by Pianka (1972) for other arid adapted lizards.

*P. microlepidota* appears to be a northern isolate derived from *P. minor mitchelli*. The two taxa are similar in most features, *P. microlepidota* being distinguished mainly by the very strongly keeled ventrals and a multiple lateral scale row. The lateral scale row similarity to *P. barbata* is puzzling. *P. microlepidota* is a little larger (maximum SVL 180mm; Storr, 1982) than *P. m.*



*mitchelli* (171mm) which is in turn larger than *P. m. minor* (145mm; Badham, 1976). These taxa thus parallel the situation in *P. vitticeps*, where southern populations are smaller (Witten & Coventry, 1990).

*P. barbata* is so similar in size to *P. vitticeps* it is easy to think of them as being close phylogenetically. However, *P. barbata* is the most derived member within the genus, having lost the second ceratobranchial (Badham, 1976) and its likely ancestry is unclear. *P. nullarbor* is apparently related, having also lost this hyoid element (Badham, 1976), and may represent a western isolate of *P. barbata*. The smaller size of *P. nullarbor* may be a further example of southern taxa being smaller than northern forms as discussed above. However, because *P. nullarbor* is nearer the presumed ancestral form in size, I favour the idea that *P. barbata* is an eastern derivative of *P. nullarbor* rather than the reverse. Another factor to consider is that *P. barbata* and *P. nullarbor* share the character of a multiple lateral scale row with *P. microlepidota*. This may indicate phylogenetic relationship, but three captive specimens of *P. nullarbor* which developed a single lateral scale row (see above) discourages heavy reliance on this feature. A complete gular scale row is a feature shared by *P. barbata*, *P. nullarbor* and *P. vitticeps*. Again this may indicate common ancestry, but is not a strong character. At our present state of knowledge the relationship of *P. barbata* and *P. nullarbor* to other members of the genus is unclear.

*Pogona* is clearly related to *Ctenophorus nuchalis*. The genus shares with this species the derived characters of a novel arrangement of preanal and femoral glands, a series of spines on the lower eyelid, and a narrow premaxilla (Witten, 1982b). The presence of these derived characters led me earlier to abandon *Pogona* as potentially ancestral to other Australian agamids. Variation within *P. minor* indicates this was an error. *P. m. minima* is more arboreal than the other subspecies, and has characteristics suggesting it may share a recent common ancestor with the *Amphibolurus* radiation (including *Lophognathus*, *Diporiphora* and *Caimanops*).

Members of the *Amphibolurus* radiation differ from *Pogona* in a number of features. They retain the presumed primitive characters of a ridge rather than spines on the paramarginal scales of the lower eyelid and a relatively wide premaxilla. The derived features which characterise *Pogona* are all less pronounced in *P. m. minima* than in other *Pogona*. The spines on the lower eyelid are

less well developed than in other taxa of *Pogona*, and some specimens approach the primitive condition where the paramarginal scales of the eyelid possess a simple ridge. The number of pleurodont teeth in *P. m. minima* is also higher at a smaller size than in *P. m. minor*, at least for dentary teeth (mean =  $4.82 \pm 0.75$ ,  $n = 11$ ; *P. m. minor* mean =  $3.44 \pm 1.05$ ,  $n = 91$ ). If this character is part of the selective trend towards *Amphibolurus* then the slightly broader premaxilla of the *Amphibolurus* radiation is a logical outcome of further selection.

Derived features characterising the *Amphibolurus* radiation include the possession of ridged labials and a peculiar pore arrangement. *P. minor* from far western continental Australia frequently have ridged labials, and *P. m. minima* usually have at least weakly ridged labials. The *Amphibolurus* pore arrangement is characterised by the preanal pores presenting in a postero-medial series more closely spaced than the femoral pores. This arrangement is found in some *P. m. minima* (Fig. 3) and *P. m. minor* from the adjacent mainland.

*Chlamydosaurus* is one of the most bizarre lizards of the world and its relationships have never been clear. Cogger (1961) included it in the *Amphibolurus* radiation, and this has been accepted in other accounts of agamid relationships (Witten, 1982a; Greer, 1989), largely on the basis of the shared pore arrangement. It lacks several of the features characteristic of the *Amphibolurus* radiation. The labials in *Chlamydosaurus* are smooth, the premaxilla is narrow, and the pore arrangement is less regular than in other members of the *Amphibolurus* radiation. A separate derivation of *Chlamydosaurus* from within *Pogona* would explain these differences. Within *Pogona* only *P. minor* from south west Australia and *P. m. minima* commonly have ridged labials, and all *Pogona* have a narrow premaxilla with 3 premaxillary teeth the maximum. The arrangement of pores in *Chlamydosaurus* is variable, and a selection of the variations in Fig. 3 could serve to illustrate the normal variation in *Chlamydosaurus*, indicating that the variation now seen in *P. m. minima* may have been shared by the original stock which gave rise to *Chlamydosaurus*.

The observed variation in *P. minor* is very interesting in the context of Australian agamid phylogeny. The pore arrangement of some *P. m. minima* closely resembles that found in *Amphibolurus* and other closely related genera. Given several other features shared by *Pogona* and *Amphibolurus*, there seems little doubt that



the *Amphibolurus* radiation arose from stock which also produced *P. m. minima*. It is remarkable that the character which typifies the *Amphibolurus* radiation more than any other should persist in a subspecies of its presumed ancestor. That several other features, such as the horizontally ridged labials, are also present in *P. m. minima* is perhaps even more remarkable. There are two possible explanations.

It is possible that the suite of characters found in the *Amphibolurus* radiation is at least originally an adaptation to more mesic conditions. The present distribution of these characters within *P. minor* may be the result of selection in the more mesic coastal parts of south western Australia. While the benefit of the derived features seen in *Amphibolurus* are unclear, it is certainly possible that they confer advantages on the coastal populations not shared by populations in arid areas. Under this hypothesis a stable cline may persist for very long periods. There has apparently not been any substantial barrier to continuous gene flow in western Australia between arid- and mesic-adapted populations.

Some indication of the period over which this cline has remained stable is given by the biochemical work of Baverstock and Donnellan (1990). Extrapolating from their figure of relationships based on differences in albumins a separation time of about 7 million years between *Pogona* and the *Amphibolurus* radiation is indicated. Given the variable rates demonstrable in albumin evolutionary rates among other agamids (Joger, 1991) this figure may need to be revised. However, the variation within the presumed derivatives of the ancestor of *Pogona minor* indicate that this is indeed an ancient cline.

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